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Research Article

Direct and indirect effects of *Gracilaria vermiculophylla* on native *Fucus vesiculosus*

Mareike Hammann[1]*, Björn Buchholz[1], Rolf Karez[2] and Florian Weinberger[1]

1 *Helmholtz-Zentrum für Ozeanforschung Kiel (GEOMAR), Düsternbrooker Weg 20, 24105 Kiel, Germany*
2 *Landesamt für Landwirtschaft, Umwelt und ländliche Räume des Landes Schleswig-Holstein, Hamburger Chaussee 25, 24220 Flintbek, Germany*

E-mail: mhammann@geomar.de (MH), bbuchholz@geomar.de (BB), Rolf.Karez@llur.landsh.de (RK), fweinberger@geomar.de (FW)

**Corresponding author*

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Abstract

The perennial red macroalga *Gracilaria vermiculophylla* (Ohmi) Papenfuss has recently been introduced to the Baltic Sea and is a potential competitor to *Fucus vesiculosus*, the most common native perennial alga in large parts of the Baltic Sea. *Gracilaria* might interfere with *Fucus* through direct competition for resources. In addition, *Gracilaria* is a favoured refuge for mesograzers, which prefer to feed on *Fucus*. Mesocosm-experiments were conducted over one year in the Kiel Fjord in order to test the direct and indirect effects of *Gracilaria* on *Fucus*. *Fucus* was incubated with *Gracilaria* at three different densities and grazers in high or low abundances. High densities of *Gracilaria* inhibited the growth of *Fucus* adults and also reduced the half-life-time of *Fucus* germlings. Associated grazers also had a negative effect on *Fucus* adults. Our results suggest that *Gracilaria* is able to influence *Fucus* in the Baltic Sea through direct competition for resources and by exposing it to higher grazer pressure.

Key words: *Fucus vesiculosus; Gracilaria vermiculophylla*; invasion biology; introduced species; algae; effects-community; Baltic Sea

Introduction

Seaweeds are frequent marine invaders (Schaffelke et al. 2006). The most common effect of invasive macroalgae in their new habitat is space monopolization that results in a reduced abundance of native species (reviewed in Schaffelke and Hewitt 2007). Loss of biodiversity and effects on fish and invertebrates were also reported (e.g. Boudouresque et al. 1992; Levin et al. 2002; Relini et al. 1998). In the case of *Caulerpa*, toxic effects on other biota were documented (e.g. Paul and Fenical 1986, reviewed in Schaffelke and Hewitt). However, most information originates from field surveys or observational studies, and there are only very few experimental studies about the impacts of invasive algae on their recipient ecosystems (Schaffelke and Hewitt 2007). As a consequence, the mechanisms underlying ecological effects of invasive species are mostly unknown (Schaffelke and Hewitt 2007). Manipulative community-level field studies, combined with modeling, are necessary to identify the impacts of introduced seaweeds on native communities (Williams and Smith 2007).

The perennial red macroalga *Gracilaria vermiculophylla* (Ohmi) Papenfuss (hereafter: *Gracilaria*) has invaded many coastal areas worldwide. From its native distribution in East Asia it has spread to other temperate areas of the northern hemisphere, primarily along both North American coasts (Bellorin et al. 2004; Freshwater et al. 2006; Thomsen et al. 2005) and in the East Atlantic between Morocco and the Western Baltic Sea (Guillemin et al. 2008; Nyberg 2007; Rueness 2005; Thomsen et al. 2007; Weinberger et al. 2008). Accounting for 74% of the entire algal biomass, *Gracilaria* dominated the shallow water habitat in Hog Island Bay, Virginia (Thomsen et al. 2006). Two recent studies show that *Gracilaria* is able to negatively impact metabolism and survival of *Zostera marina* by creating an anoxic layer (Martínez-Lüscher and Holmer 2010; Höffle et al. 2011). Possible ecological effects of *Gracilaria* on macroalgae have not been studied.

Gracilaria tolerates high irradiances and can grow in shallow water. Therefore, it is predicted to be a strong competitor for the native *Fucus vesiculosus* L. (Nyberg 2007, hereafter: *Fucus*). *Fucus* is one of the most important phytobenthic species on hard bottom habitat in the Baltic coastal zone as it provides a habitat for species-rich epiphytic and epibenthic communities (Torn et al. 2006). During the last few decades, populations of *Fucus* have declined over large areas in the Baltic Sea, most likely as a consequence of eutrophication (Torn et al. 2006). Nowadays, *Fucus* is mainly restricted to shallow water with depths between one and two meters in the western Baltic Sea (Torn et al. 2006). The presence of *Gracilaria* could increase the pressure on *Fucus* further, and observations from the Kiel Fjord indicate that *Fucus* may have declined in habitats where *Gracilaria* has spread (Weinberger et al. 2008). In the newly invaded habitats in the Baltic Sea, *Gracilaria* appears as drifting mats, sometimes partly buried in the sediment or entangled in other seaweeds or mussels. These drifting mats of *Gracilaria* overgrow both soft bottom and hard bottom substrates (Weinberger et al. 2008) and may interfere with the settlement of *Fucus* germlings and reduce the growth of adult *Fucus.*

Orrock et al. (2010) developed the idea of refuge-mediated apparent competition, i.e. an indirect interaction whereby plants provide a refuge for a shared consumer, subsequently increasing consumer pressure on another plant species. In the Baltic Sea, *Gracilaria* provides an attractive habitat for herbivores (Thomsen 2010), especially for isopods (*Idotea* spp.), which are often present at higher densities on *Gracilaria* than on *Fucus* when both algal species live in the same habitat (Weinberger et al. 2008). Noticeably, the common periwinkle *Littorina littorea* and the isopod *Idotea baltica* show a preference for consuming *Fucus* rather than *Gracilaria* when both algae are offered in two-way-choice experiments (Weinberger et al. 2008). Herbivores can exert a strong influence upon *Fucus* species (Dethier et al. 2005). In the Baltic Sea, grazing by isopods (*Idotea* spp.) and periwinkles (*Littorina* spp.) leads to biomass loss of *Fucus* (Engkvist et al. 2000; Råberg and Kautsky 2008; Torn et al. 2006). Thus *Gracilaria* may potentially influence the decline of *Fucus* through two different mechanisms, 1) directly through overgrowth and competition for resources, 2) indirectly as it provides a habitat for grazers that feed on adjacent *Fucus*.

The main purpose of our study was to investigate experimentally whether *Fucus* was affected by the presence of *Gracilaria* or by mesograzers associated with it. As life stages can be influenced differently by invaders, we focused not only on the effect of *Gracilaria* on the growth of adult *Fucus*, but also investigated the effect upon the survival of *Fucus* germlings.

Material and methods

To investigate the impact of *Gracilaria* upon *Fucus* two (for *Fucus* germlings) or seven (for *Fucus* adults) sequential experiments were conducted as seasonal repetitions. In these experiments *Fucus* was incubated with *Gracilaria* in mesocosms floating on the Baltic Sea surface. *Gracilaria* was applied at three different densities, in order to test whether its effects on *Fucus* were density dependent. The applied *Gracilaria* contained grazers at either high or low density, which allowed determining the influence of grazers. The effect of *Gracilaria* and/or associated grazers was measured as growth of adult *Fucus* specimens and as half-life time of *Fucus* germlings.

Set-up, stocking and incubation of mesocosms

The experiments were carried out in the Kiel Fjord in a sheltered bay (N54°21.965', E10°8.908') between March 2008 and March 2009. The mesocosms consisted of white polyethylene boxes (60 × 40 × 40 cm) and had a bottom made of gauze (mesh size: 1 mm) to allow for an exchange of water with the Baltic Sea but to inhibit migration of grazers. They were floating on the water surface and contained a water column of ca. 30 cm and a water volume of approximately 70 l.

Light and temperature data were provided through constant measurements of the research division “marine meteorology”, GEOMAR.

Each mesocosm was equipped with one stone with a medium-sized adult *Fucus* - devoid of grazers - and one tile with *Fucus* germlings. The chronology of the seven subsequent experiments with adult *Fucus* (hereafter: adults’ experiments), the two incubation periods of *Fucus* germlings (hereafter: juveniles’ experiments) and the environmental conditions during our studies are illustrated in Figure 1.

Adult *Fucus* individuals (mean 4.6 g WW ± 0.2 SE) growing on small stones were collected from the coastline of the Kiel Fjord. They were

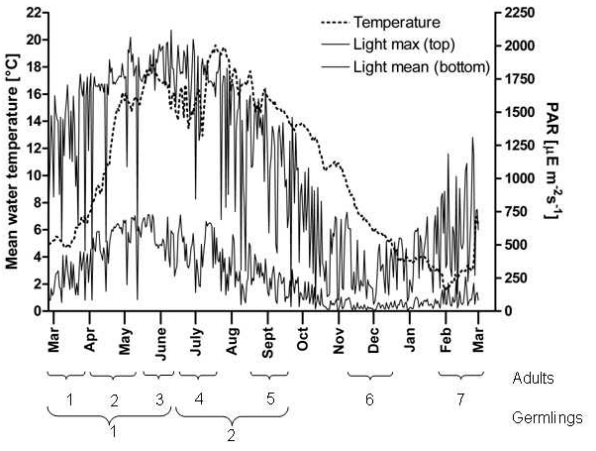

Figure 1. Development of mean water temperature in the Kiel Fjord and of mean and maximal photosynthetically active radiation (PAR) during the experiments. Also shown are the different time periods for the subsequent experiments.

replaced with newly collected specimens in the beginning of each adults' experiment. In order to obtain juveniles, tiles (15 × 15 cm) were inoculated with *Fucus* zygotes in the laboratory. One series of tiles was inoculated in January 2008 and one series in June 2008, in order to cover both reproduction periods of *Fucus* in the Baltic Sea (Berger et al. 2001). The winter germlings had an age of approximately 50d when they were transferred to the mesocosms for the first juveniles' experiment. The summer germlings were only 10 days old when the second juveniles' experiment started, but due to lower growth rates in winter the initial size of germlings was similar in both experiments (approximately 10 cells).

There were three different *Gracilaria* density treatments with ten replicates each (Figure 2): **No** *Gracilaria*, *Gracilaria* at a **low** density (5 – 10% of the 0.24 m² bottom of the mesocosm covered with *Gracilaria*, equalling 100 g of biomass FW) and *Gracilaria* at a **high** density (100 % covered, equalling 1000 g FW). These densities were considered relevant since *Gracilaria* ground coverage of up to 100% was previously observed in certain areas of the Kiel Fjord (Weinberger et al. 2008). For stocking, *Gracilaria* from drifting mats was collected together with its associated grazers with a dip net (mesh size 0.1 mm) in shallow parts of the Kiel Fjord.

Each of the three *Gracilaria* density treatments was conducted in five mesocosms with low grazer density and in five mesocosms with high grazer density (Figure 2). In mesocosms containing no *Gracilaria* the natural density of grazers associated with *Fucus* collected in nature was regarded as high, while absence of grazers was regarded as low. The natural grazer density on *Fucus* was determined prior to each experiment by counting all grazers that were present on five *Fucus* specimens collected with a gauze net (mesh size 0.1 mm) and comparable densities of grazers were added into mesocosms without *Gracilaria*, but with high grazer density (Figure 2).

In mesocosms containing *Gracilaria* the natural density of grazers in *Gracilaria* mats was considered as high, while an artificially reduced density was considered as low. For reduction of grazer densities half of the *Gracilaria* stocking material was treated with freshwater for two hours. This procedure resulted in the removal of a part of the associated grazers and thus generated low grazer densities. Preliminary tests had confirmed the efficiency of this method. Moreover, a control experiment was conducted after each freshwater treatment, in order to ascertain that *Gracilaria* was not affected. For this purpose, six samples of freshwater treated and six samples of untreated *Gracilaria* (10 g each) – in both cases grazers had been manually removed - were incubated in single mesh bags (mesh size: 1 × 1 cm) at 15°C and under artificial light in the same aquarium, provided with sea water from the Baltic Sea. After seven days the growth of treated and untreated *Gracilaria* was determined and the effect of the two treatments was compared. No significant differences between treated and untreated *Gracilaria* were found in any of the experiments (Mann-Whitney-U-test, $p > 0.05$). Thus, the freshwater-treatment had no detectable effect upon the growth of *Gracilaria*.

Prior to the start of each experiment the initial density of grazers associated with *Gracilaria* stocking material was determined by taking samples of untreated and freshwater treated *Gracilaria* with a dip net. The samples were fixed with formaldehyde in seawater (4%) and the grazers were picked under a stereo microscope, classified and counted.

In order to reduce the impact of fouling organisms attached to the mesocosm walls, they were replaced with clean mesocosms in the

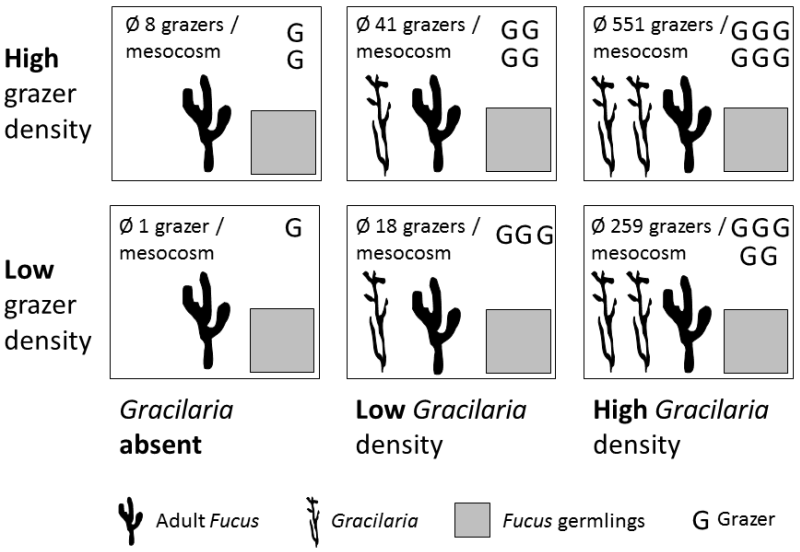

Figure 2. Experimental set-up. Three *Gracilaria vermiculophylla* densities (without, high and low) were combined with two grazer densities (low and high).

beginning of each adults' experiment. At these occasions *Gracilaria* was also removed and replaced with either 100 g or 1000 g of newly collected *Gracilaria* from the Kiel Fjord, either treated with freshwater or not, as described above. In contrast, tiles bearing *Fucus* juveniles were kept over several adults' experiments (see Figure 1), and transferred into the newly stocked mesocosms.

Sampling collection

For growth measurements, adult *Fucus* individuals were cleaned and spread under a plexiglass panel and photographed beside a benchmark in the beginning and at the end of each adults' experiment. The photos were evaluated by using a computer imaging program (Sigma Scan Pro, STATCON, Witzenhausen, Germany) which counted pixels representing the benchmark area and *Fucus*, thus allowing for calculation of the algal surface area.

Four times during each juveniles' experiment the germlings attached to tiles were counted by microscopy – in the beginning, the end and two times during the experimental run.

Animals present in the mesocosms were fixed with formaldehyde (4%) at the end of each adults' experiment. They were identified and counted under a stereo microscope. In mesocosms without *Gracilaria* and in mesocosms with *Gracilaria* at low density all grazers were quantified, while subsamples (90 ± 36 g FW) were analyzed from mesocosms containing *Gracilaria* at high density.

We only considered potential grazers of *Fucus* for our analysis. In the Kiel fjord and adjacent waters these are the periwinkle *Littorina* spp., and the isopods *Idotea* spp., *Sphaeroma rugicauda* and *Jaera albifrons* (Sjöberg 1967; Frier 1979; Weinberger et al. 2008; hereafter: *Littorina*, *Idotea*, *Sphaeroma*, *Jaera*). *Idotea* and *Littorina* prefer to consume *Fucus* rather than *Gracilaria* in two-way-choice experiments (Weinberger et al. 2008).

Comparison of the grazer densities in single mesocosms at the beginning and at the end of adults' experiments revealed that the intended adjustment of grazer densities was largely effective. However, small isopods proved able to migrate into the mesocosms in summer and *Littorina* densities sometimes declined due to escape, but mesocosms intended to contain grazers at high and low densities generally still showed this difference at the end of each adults' experiment. However, in adults' experiment 3, 4, 5 and 7 real and intended grazer densities did not fully correspond. Thus mean values of effective grazer densities at the beginning and at the end of each experiment were calculated for each mesocosm and for each of the main grazer genera. Afterwards, the five mesocosms with

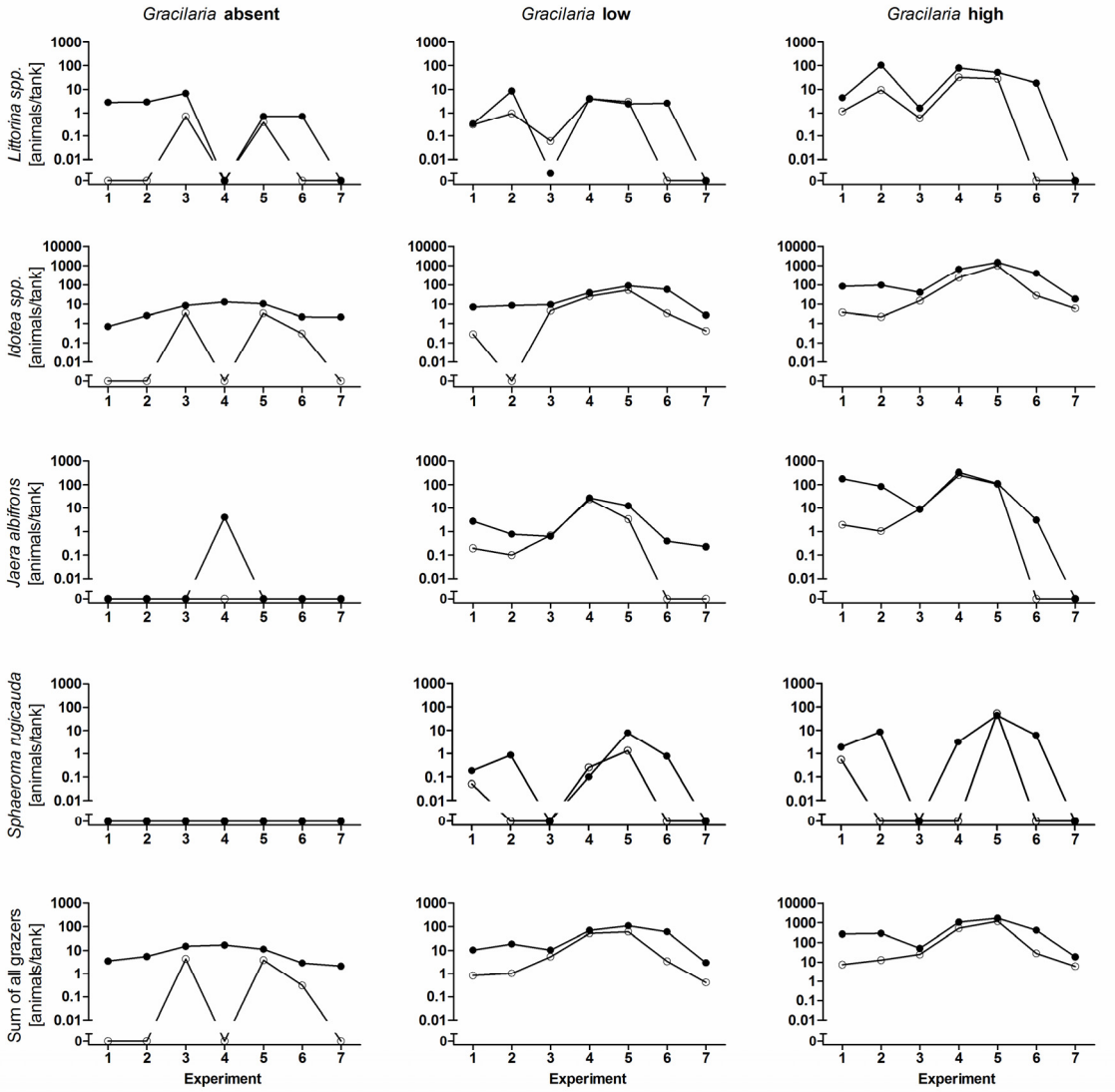

Figure 3. *Littorina spp., Idotea spp., Jaera albifrons,* and *Sphaeroma rugicauda*. Mean densities in mesocosms with high or low *Gracilaria vermiculophylla* density or without *Gracilaria* and with low (○) and high (●) grazer densities during seven single adults' experiments, n = 5.

relatively high and the five mesocosms with relatively low mean grazer density had to be chosen *post hoc* for each *Gracilaria* density. The real mean grazer densities in the two juveniles' experiments were calculated based on grazer densities determined in the beginnings and ends of adults' experiments 1 to 3 (which together covered the time window of juveniles' experiment 1, see Figure 1) and adults' experiments 4 and 5 (covering juveniles' experiment 2, see Figure 1), respectively. Real and intended grazer densities fully corresponded in juveniles' experiment 1, while a *post hoc* distinction of mesocosms with relatively low and relatively high grazer density was necessary in juveniles' experiment 2. Figure 3 shows average grazer densities (i.e. mean values of grazer densities at the beginning and at the end of each experiment in five replicate mesocosms) in the course of the different experiments and in the different *Gracilaria* treatments for both high and low grazer treatments as assigned by us *post hoc*.

Data analysis

Computation of half-life times of *Fucus* germlings

Using the "Prism 4.03"-software (GraphPad Software, La Jolla, Ca., USA.), an exponential decay function was fitted by adaptive iteration to the densities of *Fucus* germlings that were observed at successive countings. The function used was $Y=B\times e^{(-K\times X)} + A$, with Y = germling density at a given time X, A = final germling density, B = maximal decrease of germling density, K = rate constant. In this way the half-life time Z of the germlings on each tile could be estimated, using the function $Z = 0.69/K$.

ANOVA and post-hoc tests

The effect of *Gracilaria* density, grazer density and the respective experimental period upon the half-life time of *Fucus* germlings and the growth of *Fucus* adults was tested for significant differences, using factorial ANOVA and Tukey's post-hoc test. Prior to statistical tests, all data were rank-transformed, as this transformation best reduced heteroscedasticity. In the adults' data set, homogeneity of variances could not be achieved for the factor "time" (Levine's test, $p < 0.05$) and results were taken as statistically significant if the probability of type I error was less than 1% (Underwood 1997), while other results were taken as statistically significant at a p-level of 5%.

Results

Seasonal variation in environmental conditions

The environmental conditions followed a typical seasonal pattern (see Figue 1). Low temperatures of < 5°C were characteristic for the winter months, while peak temperatures of 20°C were reached in July and August. Light intensity was already relatively high in spring and slowly increased until June. Lowest light intensities were measured in December and January. In December and January there are only 7 h of daylight compared with 17 h in June and July.

Growth of adult Fucus individuals

Not surprisingly, the time when an experiment was carried out had a significant effect on the growth of *Fucus* adults ($p<0.001$; see Table 1 and Figure 4). Growth rates were highest in May/June (experiment 3), whereas the weight of *Fucus* declined in November/December (experiment 6) and moderate growth rates were achieved in spring and autumn (experiments 1, 2, 4, 5, 7). Also the presence of *Gracilaria* had a significant effect upon the growth of *Fucus* adults (Table 1 and Figure 5). The post-hoc test detected that presence of *Gracilaria* at high density resulted in significantly ($p<0.001$) less *Fucus* growth than presence at low density or absence. Grazers alone had no significant effect on the growth of *Fucus* at the chosen alpha level ($p=0.053$, Table 1), but ANOVA detected a significant interactive effect of *Gracilaria* density and grazer density ($p<0.01$, see Tab. 1 and Figure 5). At low *Gracilaria* density the presence of high grazer densities significantly reduced *Fucus* growth, while grazer treatments did not affect growth at other *Gracilaria* densities. This interactive effect was particularly obvious in April/May (experiment 2; see Figure 4) and from July to December (experiments 4, 5, 6; see Figure 4).

Development of germlings

During the first experimental period from March to June, the average initial density of *Fucus* germlings on tiles was 231.1 cm^{-2}, while their average half-life was 1.40 ± 0.07 weeks (mean ± S.E.). The average initial *Fucus* density during the second experimental period from June to September was lower than in the first period (36.9 germlings cm^{-2}). The average half-life time (mean ± S.E.: 0.45 ± 0.06 weeks) was also significantly shorter than in the first experiment ($p<0.001$; Table 2 and Figure 6). Based on ANOVA results the factor "*Gracilaria*" also significantly influenced the survival of germlings ($p<0.001$; Table 2). Half-life time was longest in treatments with low *Gracilaria* density and shortest in treatments with high *Gracilaria* density (Figure 7). Grazers had no significant effect upon the half-life time of *Fucus* germlings (Table 2 and Figure 7).

Discussion

The main purpose of the experiments was to test the two hypotheses (1) that *Gracilaria* affects *Fucus* directly and (2) that mesograzers associated with *Gracilaria* have an impact on *Fucus*. Both hypotheses cannot be rejected. *Gracilaria* had an influence on adult *Fucus* individuals and *Fucus* germlings. High *Gracilaria* densities

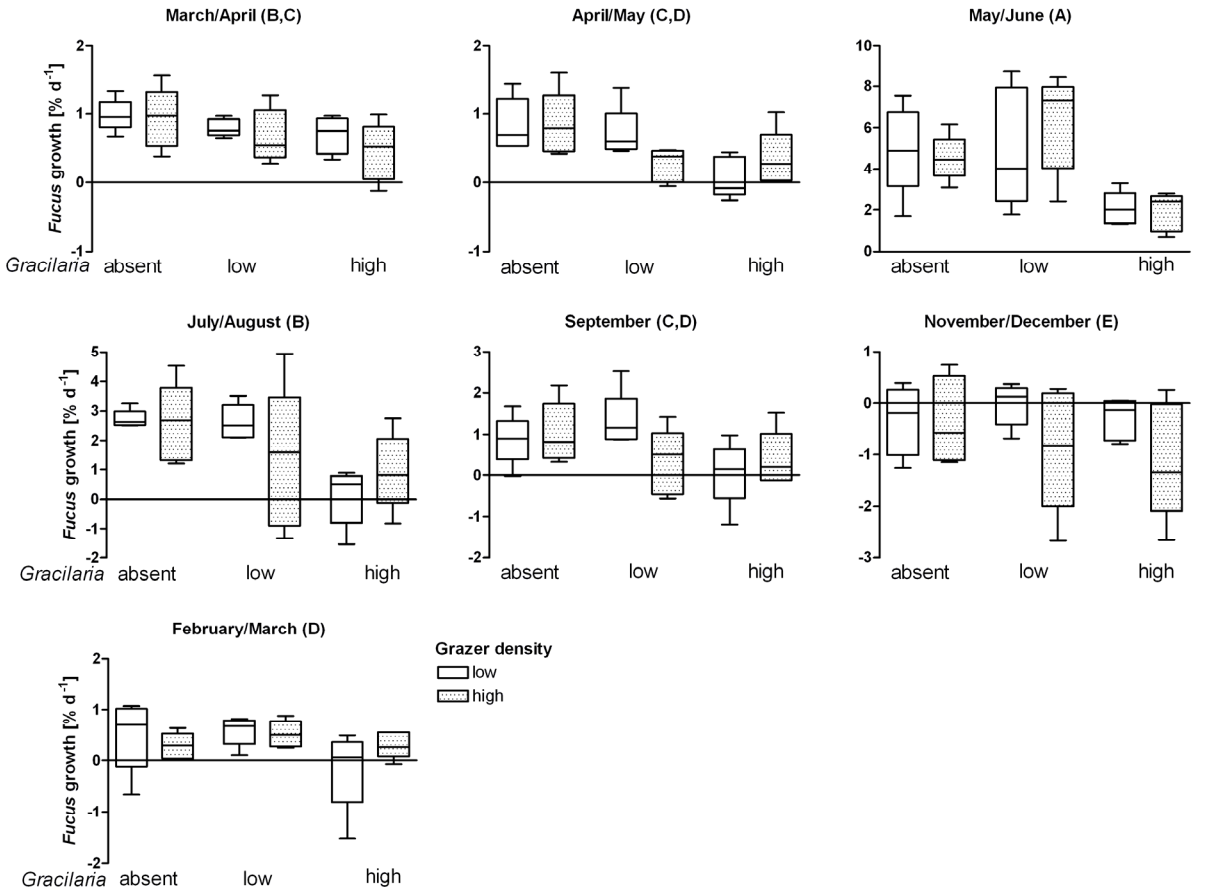

Figure 4. *Fucus vesiculosus*, adults. Growth in mesocosms with high or low *Gracilaria vermiculophylla* density or without *Gracilaria*, and with low or high grazer densities. Single results of seven successive experiments, n = 5. Different letters in the graph titles indicate the experiments that were significantly different in a Tukey-test ($p < 0.01$).

clearly reduced the half-life time of *Fucus* germlings and growth of *Fucus* adults as compared to low *Gracilaria* densities. Grazers only had an effect on *Fucus* adults at low *Gracilaria* densities.

Growth of adult Fucus

There was a significant seasonal variation in *Fucus* growth, as would be expected. Growth rates were highest in May/June when water temperature and light availability were elevated. With low water temperatures and reduced light availability in November/December, *Fucus* biomass declined.

Fucus adults grew least when *Gracilaria* was present at high density, but there was no difference in growth when *Gracilaria* was absent or present at low density. At high density the ground coverage by *Gracilaria* was 100 %, and one can assume that such conditions result in a reduced availability of light, oxygen and nutrients for *Fucus*, despite its capacity to protrude *Gracilaria* mats due to the buoyancy provided by gas filled bladders. Also, an allelopathic effect cannot be excluded.

Grazers reduced the growth of *Fucus* as well, but the overall effect was relatively small in size (a reduction of growth by approximately 8%) and statistically not significant. It is possible that epiphytes and other fouling organisms may have interfered with the interactions of *Gracilaria, Fucus* and grazers. Especially in spring and early summer ephemeral algae - first *Ulothrix* spp. and later tube forming diatoms - were present on mesocosm walls and entangled in *Gracilaria* and

Table 1. Growth of *Fucus vesiculosus* adults. Effect of time when an experiment was conducted, *Gracilaria vermiculophylla* density and grazer density in a fully factorial ANOVA.

	SS	*DF*	*MS*	*F*	*p*
Time	407493	6	67915	53.08	<0.001
Gracilaria	65402	2	32701	25.56	<0.001
Grazer	4867	1	4867	3.80	0.053
Time**Gracilaria*	20195	12	1683	1.32	0.21
Time*Grazer	1740	6	290	0.23	0.97
*Gracilaria**Grazer	14116	2	7058	5.52	<0.01
Time**Gracilaria**Grazer	21118	12	1760	1.38	0.18
Error	211136	165	1280		

Table 2. Half-life time of *Fucus vesiculosus* germlings. Effect of time when an experiment was conducted, *Gracilaria vermiculophylla* density and grazer density in a fully factorial ANOVA.

	SS	*DF*	*MS*	*F*	*p*
Time	10837.26	1	10837.26	120.15	<0.001
Gracilaria	1027.03	2	513.51	5.69	<0.01
Grazer	3.60	1	3.60	0.04	0.84
Time**Gracilaria*	129.79	2	64.90	0.72	0.49
Time*Grazer	76.18	1	76.18	0.84	0.36
*Gracilaria**Grazer	26.75	2	13.37	0.15	0.86
Time**Gracilaria**Grazer	21.30	2	10.65	0.12	0.89
Error	4149.20	46	90.20		

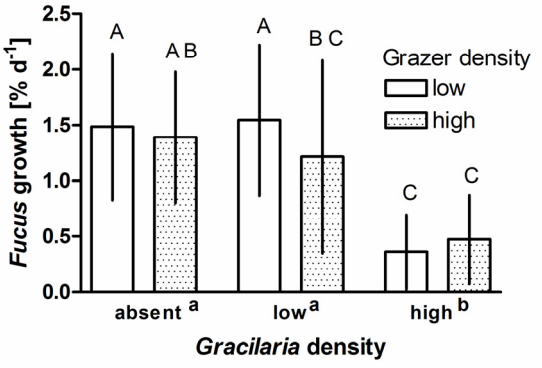

Figure 5. *Fucus vesiculosus*, adults. Growth in mesocosms with high or low *Gracilaria vermiculophylla* density or without *Gracilaria,* and with low or high grazer densities. Mean of seven successive experiments ± 95% CI, n = 35. Different lower-case letters indicate *Gracilaria* treatments that were significantly different in a Tukey-test ($p < 0.05$), while upper-case letters indicate differences in the interactive effect of *Gracilaria* and grazers ($p < 0.05$).

on *Fucus*. These algae were also observed in spring and early summer on *Gracilaria* and on *Fucus* in nature. Several experiments have shown that many grazers (including *Idotea*) preferably feed on epiphytes and ephemeral algae, also those growing on *Fucus* (Karez et al. 2000; Orav-Kotta and Kotta 2004; Worm and Sommer 2000). Preferential consumption of ephemeric algae might thus reduce the negative effect of mesograzers upon *Fucus*.

The effect of grazers on *Fucus* differed with *Gracilaria* density. Treatments with high grazer density contained for both *Gracilaria* densities (low and high) roughly the double amount of grazers as treatments with low grazer density (see Figure 2 and Figure 3). High *Gracilaria* densities had the strongest negative impact on *Fucus* growth rates, irrespective of grazer density. Thus *Gracilaria* biomass clearly is of higher importance for *Fucus* growth than the grazers associated with it. Any effects of grazers are probably superimposed by effects of *Gracilaria* in high density. In contrast, at low *Gracilaria* density an increased density of grazers resulted in decreased *Fucus* growth. This

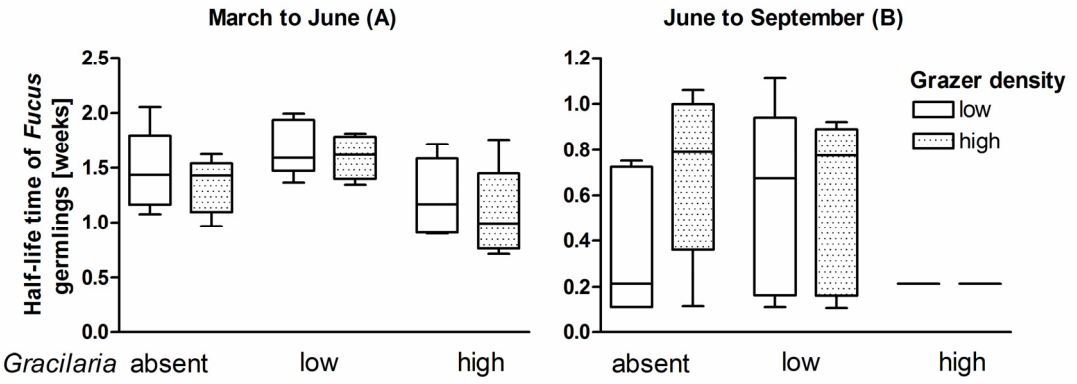

Figure 6. *Fucus vesiculosus*, germlings. Mean half-life time in mesocosms with high or low *Gracilaria vermiculophylla* density or without *Gracilaria* and with low or high grazer densities. Single results of two successive experiments, n = 5. Different letters in the graph title indicate that the experiments were significantly different in a Tukey-test ($p < 0.05$).

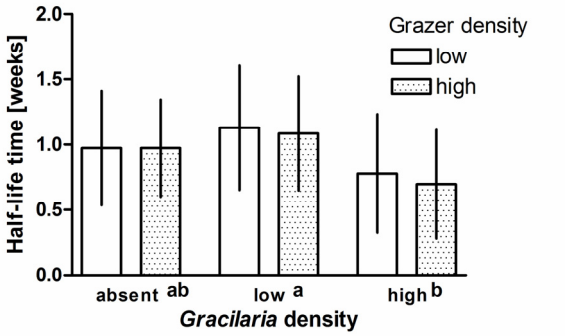

Figure 7. *Fucus vesiculosus*, germlings. Mean half-life time in mesocosms with high or low *Gracilaria vermiculophylla* density or without *Gracilaria* and with low or high grazer densities. Mean of two successive experiments ± 95% CI, n = 10. Different letters indicate treatments that were significantly different in a Tukey-test ($p < 0.05$).

was not the case in absence of *Gracilaria*, where *Fucus* growth was generally high and again unaffected by grazers. *Fucus* in *Gracilaria* free environments is occasionally heavily grazed (Dethier et al. 2005; Engkvist et al. 2000), but the natural densities of grazers associated with *Fucus* during the experimental periods were too low to cause a significant decline in *Fucus* growth. Grazers thus affected growth only at low *Gracilaria* density. This indicates that the grazer population accommodated by *Gracilaria* poses an additional indirect threat to *Fucus*. However, the effect only gets visible when the direct effects of *Gracilaria* are relatively small.

Development of germlings

The early live stages of *Fucus* are generally especially vulnerable (Berger et al. 2003). In our experiments, germlings were found to have the shortest half-life time when *Gracilaria* was present at high density. This effect was especially pronounced in the second experimental period where none of the *Fucus* germlings survived at high *Gracilaria* treatments – irrespective of grazer density. Buried under thick *Gracilaria* mats, the germlings presumably suffered from a reduced availability of light and oxygen. However, both generations of *Fucus* germlings also tended to have a slightly longer half-life time in presence of *Gracilaria* at low density than in absence of *Gracilaria*, suggesting that *Gracilaria* may have both positive and negative effects upon the survival of *Fucus* germlings. In other experiments, low concentrations of *Pilayella littoralis*-exudates had a positive effect on the germination of *Fucus* zygotes (Råberg et al. 2005). This effect was attributed to the enhanced nutrient concentration in the exudates, which probably supported the germlings. Possibly, *Fucus* germlings in mesocosms with low *Gracilaria* density also profited from a slightly raised nutrient concentration, but other explanations can also not be excluded.

Ecological consequences and outlook

With some restrictions, the results of our mesocosm experiments can be compared to natural processes. The densities of both *Gracilaria*

and grazers were based on those found in nature. Also the water depth was similar to that in nature, as both species occur mainly in shallow water in the Kiel Fjord.

Growth of *Gracilaria* in the southwestern Baltic is limited by light and largely restricted to summer and water depths above 3m (Weinberger et al. 2008). With *Fucus* appearing in similar depths of water, there could be a strong competition for space and light between the two species (Nyberg 2007). Based on our studies, *Gracilaria* appears to be able to restrict growth of *Fucus* in these shallow waters. Especially in sheltered bays with little water fluctuation and where high densities of *Gracilaria* can amass, the effect of *Gracilaria* on *Fucus* could be detrimental, even though it will presumably not lead to the extinction of single populations. The further effects, however, depend very strongly upon how *Gracilaria* influences the settlement and development of *Fucus* germlings. Our experiments show that in dense *Gracilaria* mats with numerous grazers, the survival of *Fucus* germlings approaches zero. The local density of *Gracilaria* in nature therefore is a crucial factor that determines which effect the presence of *Gracilaria* actually has. Other factors such as deposited matter trapped in algal mats have also to be taken into consideration in order to estimate the overall impact of *Gracilaria* upon *Fucus*. Furthermore, it has to be held that the results of the experiments conducted cannot be applied to the entire Baltic Sea without reservations, but first and foremost to the western Baltic Sea with its special conditions of salinity, light and temperature.

Currently, *Gracilaria* appears in the German Baltic Sea mainly in its unattached form. However, the species seems to be capable of sexual reproduction at relatively low salinities (own observations). Should *Gracilaria* recruits settle on hard substrate, the competition for space with *Fucus* germlings might increase even further. Space occupation by other algae has been shown to have a strong negative effect on the settling success of spores and zygotes (Vadas et al. 1992), also those of *Fucus* ssp. (Berger et al. 2003; Råberg et al. 2005; Steen 2004; Worm and Chapman 1996). In the long run, a rise of water temperatures as a consequence of global warming might intensify the competitive situation in the Baltic Sea (Leppäkoski et al. 2002; Stachowitz et al. 2002), because *Gracilaria*, unlike *Fucus,* grows even better at higher temperatures (Yokoya et al. 1999).

Gracilaria appears to show an exceedingly strong potential of changing the habitat in which it grows. It alters the habitat architecture by forming thick mats. Thereby it works as a trap for sediment and other particles and shades other algae (Nyberg 2007).

On the other hand, *Gracilaria* in small amounts adds structural complexity to a relatively homogeneous system. It sustains a large taxonomic richness and provides a new habitat for many taxa (Nyberg 2007; Thomsen 2010). Our experiments were conducted in an environment of relatively low diversity (Rönnbäck et al. 2007), but 18 different animal taxa were nonetheless found in *Gracilaria* (data not shown).

Thomsen et al. (2012) found out that *Gracilaria comosa* had ambiguous effects in its new environment in Australia, as it inhibited the native seagrass *Halophila ovalis* itself, but facilitated most seagrass-associated invertebrates. Accordingly, the question should be asked, whether *Gracilaria*, which in fact harbours a high biodiversity, could be an adequate replacement for *Fucus* in the Western Baltic Sea if the decline of the latter continues or whether consequences of a further spread of the invader would rather be detrimental for the system. Kraufvelin and Salovius (2004) stated that substitution of *Fucus* by the filamentous green alga *Cladophora glomerata* does not immediately affect macroinvertebrate diversity negatively. Other authors also found out that following a decline of *Fucus* the majority of *I. balthica* switched to an alternate habitat (Orav-Kotta and Kotta 2004). Weinberger et al. (2008) postulated a possible functional replacement of *Fucus* by *Gracilaria* and a gain of habitat for seaweed associated organisms on soft bottom substrates. However, while animal abundances and biomass are higher in *Gracilaria* as compared to *Fucus* - probably due to the finer morphology of *Gracilaria* - epiphytic algae and sessile epiphytic animals are generally more abundant on fucoids and may lose substrates if *Fucus* is replaced by *Gracilaria*. Thereby, the habitat complexity may be reduced and energy fluxes may be affected (Kraufvelin and Salovius 2004). A decline of *Fucus* might for similar reasons be harmful to the stability of the whole community (Torn et al. 2006). Moreover, high densities of algal mats stress benthic communities directly, especially by creating oxygen deficiency (Arroyo et al. 2012; Berezina and Golubkov 2008; Norkko and Bonsdorff 1996; Norkko et al. 2000) and even night-time anoxia caused by rapid algal growth in the summer (e.g. Shen et al. 2008). In

conclusion, opportunistic and mobile taxa may benefit from algal mats consisting of *Gracilaria*, but stenoecious key species adapted to *Fucus* may be lost, and fundamental changes to community function and food web might be induced.

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